

GYNANDROMORPHISM IN POLLINATING FIG WASPS (HYMENOPTERA: AGAONIDAE)¹

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ABSTRACT: Gynandromorph specimens of pollinating fig wasps (Hymenoptera: Agaonidae) are reported for the first time. Gynandromorph individuals of *Pegoscapus tonduzi* (pollinator of *Ficus citrifolia* - Moraceae) and *Blastophaga psenes* (pollinator of *F. carica*) were found in galls from which insects had not emerged. *P. tonduzi* gynandromorph specimens showed female and male tissues distributed in a mosaic over all parts of the body, but with the genitalia predominantly masculine, while in *B. psenes* the individuals had a female front part and a male hind part. The presence of gynandromorphs at low frequencies in two species suggests that they may also occur in other fig wasp species, but their occurrence is not noticed because of their low frequency and because it is necessary to crack open the closed galls to find these insects.

KEY WORDS: Agaonidae, pollinating fig wasps, Hymenoptera, gynandromorphism.

Gynandromorphism is described as the simultaneous presence within the same organism of genotypically and phenotypically male and female tissues (Laugé 1985). Gynandromorph forms have been described in several orders of arthropods (Martini et al. 1999). In Hymenoptera, this phenomenon is described within some families, such as, Anthophoridae (Urban 1999), Apidae (Gordh and Gulmahamad 1975), Chalcididae (Haltead 1988), Diprionidae (Martini et al. 1999), Formicidae (Jones and Phillips Jr. 1985), Halictidae (Nilsson 1987), Scelionidae (Huggert 1977) and others cited by Nilsson (1987).

The origin of this phenomenon is not completely known, but it is generally attributed to developmental anomalies. Nilsson (1987) discusses some possible causes of gynandromorphism in haplodiploid insects such as hymenopterans: 1) eggs that contain two nuclei and the fertilization of only one of these may produce a gynandromorph; 2) polyspermy, by which one sperm may fertilize the egg while a nucleus from a supernumerary sperm may give rise to haploid cells in the embryo and thus a gynandromorph; 3) accidental meiosis giving rise to haploid cells in a diploid embryo; 4) the opposite event giving rise to diploid cells from haploid ones and 5) accidental loss of sex-determining loci.

Feminization mediated by *Wolbachia* in genetically male individuals, although not known in Hymenoptera (Cook and Butcher 1999), deserves more studies. Feminization due to *Wolbachia* infection is known in Isopoda (Rigaud and Juchault 1993) and was recently reported in Lepidoptera (Hiroki et al. 2002, Kagayama et al. 2002). In Isopoda, *Wolbachia*-mediated feminization leads to the production of gynandromorph phenotypes (Rigaud and Juchault 1993). In Diptera, *Wolbachia* infections may be distributed throughout somatic tissues (Dobson

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et al. 1999); thus, in haplodiploid organisms like Hymenoptera, feminization associated with infection of somatic tissues could produce a gynandromorph.

The genus *Ficus* (Moraceae) is pollinated by tiny species-specific pollinating wasps belonging to the family Agaonidae (Ramírez 1970, Wiebes 1979, Herre *et al.* 1996). Agaonids show a strong sexual dimorphism, with winged females and wingless pale brown males (Figure 1 A-B). Sex-determination is haplodiploid, males developing from unfertilized eggs and females from fertilized ones (Cook 1993).

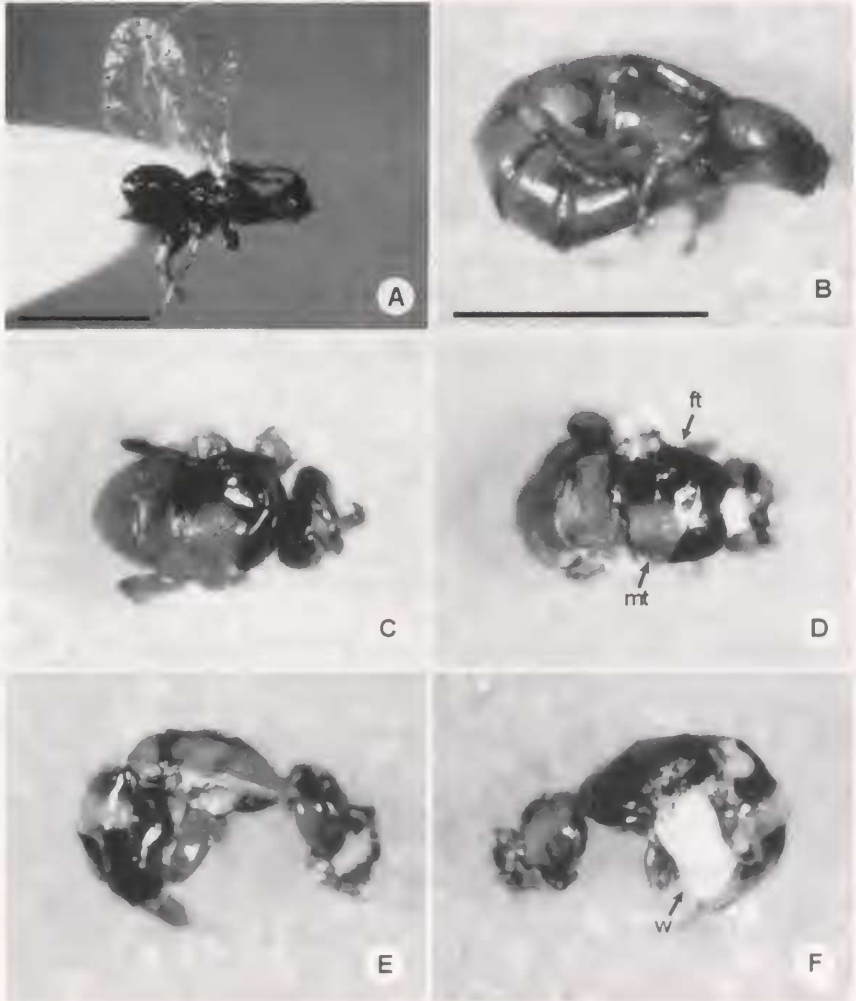


Figure 1. *Pegoscapus tonduzi* pollinator of *Ficus citrifolia*. Normal female and male: A-B. Gynandromorph individuals: C – specimen 1 (dorsal), D – specimen 2 (dorsal), E-F – specimen 3 (laterals). ft = female tissue, mt = male tissue, w = wing. B-F at the same scale. Scales = 1mm.

Among non-pollinating fig wasps, gynandromorphism was described in the genus *Psenobolus* (Ichneumonoidea, Braconidae) (Ramírez and Marsh 1996) and the gynandromorph specimen helped to associate female and male forms classified before as different species due to the accentuated sexual dimorphism. However, this phenomenon is not described in the literature for fig wasp species belonging to the superfamily Chalcidoidea that includes pollinating fig wasps.

Six gynandromorph specimens of the pollinating species, *Pegoscapus tonduzi*, were found in crops of two trees of *Ficus citrifolia* sampled during August 2001 in the surroundings of the Campinas State University campus, Brazil (22° 54'S, 47° 03'W). Twenty-five syconia of each tree were sampled near the wasp emergence phase before any wasps had left the fruit. Each syconium was placed individually in a plastic flask, and all the wasps were allowed to emerge before being frozen. The gynandromorph individuals were found in galls from which insects had not emerged, suggesting these insects had some viability problems. Gynandromorph specimens showed female and male tissues distributed in a mosaic over all parts of the body, but with genitalia predominantly masculine (Figure 1 C-F). The external morphology presented female or male traits according to the predominance of female or male tissues respectively, including the development of wings in these thorax parts with female tissues (Figure 1 F).

This phenomenon seems to be rare, since only six gynandromorph individuals were observed in approximately 600 syconia or 14,000 males assessed during the five-year study. Another interesting point is that all the gynandromorph individuals were found in two samples at the same period of the year, suggesting perhaps an environmental factor, such as low temperatures, could cause developmental interferences in these insects. Gynandromorphism was also observed, though in a slightly different form in *Blastophaga psenes*, the wasp pollinating *F. carica*. In 1984, four gynandromorphic individuals were observed in a sample of 127 syconia containing 3,312 males. They were all in non-exited galls, suggesting again a lack of viability. In *B. psenes*, the individuals had a female front part and a male hind part. Three were found on one tree within the same crop that matured in May (two in the same syconium), while the fourth was observed on another tree in a crop that matured in July. No gynandromorphic male was observed in other years of sampling.

The presence of gynandromorphs at low frequencies in two species suggests that they may occur in other fig wasp species, but their occurrences is not noticed because of their low frequency and because it is necessary to crack open the closed galls to find these insects. More studies will be necessary to elucidate the factors that lead to the development of gynandromorph fig wasp individuals.

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LITERATURE CITED

- Cook, J. M.** 1993. Sex determination in the Hymenoptera: a review of models and evidence. *Heredity* 71:421-435.
- Cook, J. M. and R. D. J. Butcher** 1999. The transmission and effects of *Wolbachia* bacteria in parasitoids. *Researches on Population Ecology* 41:15-28.
- Dobson, S. L., K. Bourtzis, H. R. Braig, B. F. Jones, W. G. Zhou, F. Rousset, and S. L. O'Neill.** 1999. *Wolbachia* infections are distributed throughout insect somatic and germ line tissues. *Insect Biochemistry and Molecular Biology* 29:153-160.
- Gordh, G. and H. Gulmahamad.** 1975. A bilateral gynadromorphic *Xylocopa* taken in California (Hymenoptera: Apidae). *Proceedings of the Entomological Society of Washington* 77:269-273.
- Haltead, J. A.** 1988. A gynadromorph of *Hockeria rubra* (Ashmead)(Hymenoptera: Chalcididae). *Proceedings of the Entomological Society of Washington* 90:258-259.
- Herre, E. A., C. A. Machado, E. Bermingham, J. D. Nason, D. M. Windsor, S. S. McCafferty, W. Van-Houten, and K. Bachmann.** 1996. Molecular phylogenies of figs and their pollinator wasps. *Journal of Biogeography* 23:521-530.
- Hiroki, M., Y. Kato, T. Kamito, and K. Miura.** 2002. Feminization of genetic males by a symbiotic bacterium in a butterfly, *Eurema hecabe* (Lepidoptera: Pieridae). *Naturwissenschaften* 89:167-170.
- Huggert, L.** 1977. Three gynandromorphic specimens of *Idris piceiventris* (Kieffer) (Hymenoptera, Proctotrupoidea: Scelionidae). *Entomologica Scandinavica* 8:158-160.
- Jones, S. R. and S. A. Phillips Jr.** 1985. Gynandromorphism in the ant *Pheidole dentata* Mayr (Hymenoptera: Formicidae). *Proceedings of the Entomological Society of Washington* 87: 583-586.
- Kageyama, D., G. Nishimura, S. Hoshizaki, and Y. Ishikawa.** 2002. Feminizing Wolbachia in an insect, *Ostrinia furnacalis* (Lepidoptera : Crambidae). *Heredity* 88:444-449.
- Laugé, G.** 1985. Sex determination: Genetic and epigenetic factors. *In*, Comprehensive insect physiology biochemistry and pharmacology, vol. 1. Embryogenesis and reproduction. G. A. Kerkut and L. L. Gilbert (Editors), Pergamon Press, Oxford, England. 487 pp.
- Martini, A., N. Baldassari, and P. Baronio.** 1999. Gynandromorphism and its manifestations in Diprionid Hymenoptera. *Bollettino dell'Istituto di Entomologia "Guido Grandi." dell'Università di Bologna* 53:87-107.
- Nilsson, G. E.** 1987. A gynandromorphic specimen of *Evylaeus albipes* (Fabricius)(Hymenoptera, Halictidae) and a discussion of possible causes of gynandromorphism in haplo-diploids insects. *Notulae Entomologicae* 67:157-162.
- Ramírez B. W.** 1970. Host specificity of fig wasps (Agaonidae). *Evolution* 24:680-691.
- Ramírez B. W. and P. M. Marsh.** 1996. A review of the genus *Psenobolus* (Hymenoptera: Braconidae) from Costa Rica, an inquiline fig wasp with brachypterous males, with descriptions of two new species. *Journal of Hymenoptera Research* 5:64-72.
- Rigaud, T. and P. Juchault.** 1993. Conflict between feminizing sex-ratio distorters and an autosomal masculinizing gene in the terrestrial isopod *Armadillidium vulgare* Latr. *Genetics* 133:247-252.
- Urban, D.** 1999. Ginandromorfia em *Alloscirtetica brethesi* (Joergensen) (Hymenoptera, Anthophoridae). *Revista Brasileira de Zoologia* 16: 171-173.
- Wiebes, J. T.** 1979. Co-evolution of figs and their insect pollinators. *Annual Review of Ecology and Systematics* 10:1-12.